Latitudinal patterns in body size of Roesel's bush cricket *Metrioptera roeselii* within and outside the continuous area of its distribution

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Sammanfattning

Människans ökade resande och transport av organismer har lett till att fler och fler främmande arter etablerar sig på nya platser och de kan påverka den nya miljön negativt. Till exempel tror man att cikadavårtbitaren i Sverige utkonkurrerar den inhemska ljungvårtbitaren, *Metrioptera brachyptera*. Det är därför viktigt att ta reda på hur cikadavårtbitaren som en koloniserande art klarar sig. Resultaten från denna studie kan användas när man behöver kunskap om hur en främmande art etablerar sig och om processer hos koloniserande främmande arter.

Cikadavårtbitaren, *Metrioptera roeselii*, är en liten och kortvingad art på 12- 18 mm. Färgen varierar från ljusbrun till klargrön, men det mest karaktäriska är den ljusa randen på halsskölden. Den föredrar fuktiga obetade gräsmarker med högt gräs och födan består av gräs, gräsfrön och små insekter. Cikadavårtbitaren är en vanlig och utbredd art i den kontinentala delen av Europa medan den i Skandinavien är relativt nyligen etablerad. Man tror att cikadavårtbitaren kom till Sverige som medpassagerare i lastfartyg eller som ägg på flytande växtmaterial över Östersjön. Antalet populationer ökar och den förekommer idag isolerat i Skåne (Smygehuk), Mälardalen samt på enstaka platser utmed norrlandskusten (Skellefteå, Umeå, Luleå och Haparanda).

Populationerna i Sverige, i Danmark och på öarna i Östersjön kan betraktas som isolerade eftersom Östersjön separerar dem från artens kontinuerliga utbredning. När få individer grundar en ny population representerar de en mindre del av den genetiska variation som finns i den ursprungliga populationen. Om en sådan population förblir liten och dessutom avskärmad från andra populationer kan det leda till inavel och i förlängningen inaveldepression, vilket påverkar fitness negativt. Det kan till exempel betyda minskad kroppsstorlek. Min arbetshypotes är att de isolerade populationerna utanför artens kontinuerliga utbredning lider av inavelsdepression och att det kommer till uttryck i att de är mindre än de individer som finns inom artens kontinuerliga utbredning. För att ta reda på detta jämförde jag morfologiska karaktärer mellan individer insamlade från dessa två grupper av populationer.

Resultaten visade att individerna i de isolerade populationerna inte alls var mindre än de i kontinuerliga utan snarare var större. Resultaten visade också att de isolerade individerna ökade i storlek med högre latituder medan de kontinuerliga var lika stora oavsett latitud. Detta kan bero att isolerade populationer inte hade kontakt med varandra och därför kan evolvera till sina ekologiska optima medan de kontinuerliga påverkas av invandrande individer från andra delar av dess utbredningsområde, där de lokala förutsättningarna är annorlunda. Att individerna är större i norr respektive i de isolerade populationerna kan bero på kroppscellerna tillåts växa sig större i kallt klimat och att de har större tillgång på föda där konkurrensen är lägre. Cikadavårtbitaren är en allätare och konkurrenskraftig, och verkar således klara den isolerade situationen bra.

Abstract

Over time, species colonize new areas naturally or through humans. The colonizers are often few and founded populations represent only a fraction of the genetic diversity existing in the original population. If the established population becomes isolated after the colonization event genetic diversity will remain low and if the population, in addition, remains small in size for an extended period this will lead to increased inbreeding and possibly inbreeding depression. *Metrioptera roeselii* is a common species with a widespread distribution in continental Europe. During the last century, it has expanded to the Scandinavian Peninsula which is separated from continental Europe by the Baltic Sea. My aim was to test the hypothesis that individuals in isolated populations in Scandinavia including Denmark and the Baltic Sea islands are smaller than individuals in the continuous part of its distribution due to low genetic diversity and lacking incoming gene flow. I measured and analyzed ten morphological traits and found no support for my hypothesis. Rather, no trait in the isolated populations was smaller than in continuous ones but was instead on average larger. To control for the influence of regional climate, *distance to coast* and *latitude* were included as factors and both explained a large part of the trait variation in the isolated populations while they did not in continuous ones. My conclusion is that *M. roeselii* manages the isolated situation well because it is a generalist and good competitor. Differences in gene flow among the two groups of populations lead to different latitudinal pattern with increasing body mass at higher latitude in isolated populations while in continuous populations, they were of equal size.

Introduction

Species naturally colonize new areas (di Castri *et al.*, 1989) and there are several processes affecting species distribution patterns. For example, the climate fluctuates and species respond through changing their distribution area (Hewitt, 1999). In addition, habitat availability, dispersal ability, interactions with other species (e. g. competitors and disease organisms), population dynamics and barriers to dispersal determine a species occurrence (Pearson, Dawson, 2003; Ricklefs, 2007). Due to increased human movement and activity, the number of species that have spread to new areas has increased in recent history (di Castri *et al.*, 1989), when introduced as game, for biological control, for aesthetic purposes or by mistake as stowaways (Armstrong, 1982; den Hartog, van der Velde, 1987; Le Hénaff, Crête, 1989; Mayr, 1964; Roots, 1976).

Individuals that colonize new areas are often few and represent only a small part of the genetic diversity existing in the original population, i.e. founder effect. Small populations are more affected by genetic drift, which will lead to even more reduced genetic variation, i.e. bottleneck effect, through random sampling of genotypes to the following generations (Ricklefs, 2007). If the population remains small for an extended number of generations individuals will also become increasingly related and the level of inbreeding will increase (Ricklefs, 2007). This can lead to inbreeding depression (Roff, 1997) when related individuals mate and shared deleterious alleles are expressed (Ricklefs, 2007). This can affect body size (Fredickson, Hedrick, 2002) as well as fitness (Reed *et al.*, 2003; Roff, 1997). Inbreeding depression is well documented among many insects (Fox *et al.*, 2007; Henter, 2003; Luna, Hawkins, 2004; Reale, Roff, 2003; Roff, 2002; Saccheri *et al.*, 2005) with responses such as impaired egg development and hatching, impaired larval survival, reduced nymph weight and fewer offspring.

Roesel's bush cricket, *Metrioptera roeselii*, is a common species in continental Europe. During the last century, its distribution area has increased and today *M. roeselii* can be found in areas where it did not occur before (Bavnhoj, 1996; de Jong, Kindvall, 1991; Delphin, 1983; Pettersson, 1996; Simmons, Thomas, 2004). The populations found in the Scandinavian Peninsula, Denmark and the Baltic Sea islands are more or less recently founded and are considered as isolated. These isolated populations allowed me to investigate how founder events and isolation affect the performance of this species. The continuous occurrence in the Baltic States and in most of parts of Finland in combination with the isolated populations beyond this area creates a unique opportunity to evaluate the influence of founder events and isolation on the performance of an invading species controlling for latitudinal effects. I use the body size as an indicator of inbreeding depression since size is easy to evaluate compared with the other indicators like egg development and hatching, larval survival and number of offspring which would require lab work and this was beyond the timeframe of my thesis. However, size is likely to be correlated with overall fitness, and changes in the mean body size can therefore reflect inbreeding depression (Bryant *et al.*, 1986). Examples of when body trait sizes were correlated with inbreeding are losses in heritability of wing area of the butterfly *Bicylus anynana* (Saccheri *et al.*, 2001), reduced mean dry weight of the house fly *Musca domestica* (Bryant *et al.*, 1986), smaller mean wing size of several wasps (Kölliker-Ott *et*

al., 2003) and slower development speed of the cowpea seed beetle, *Callosobruchus maculatus* (Tran, Credland, 1995). Therefore, I hypothesises that individuals in the isolated populations are smaller than the ones in the continuous populations due to low genetic variation and inbreeding depression due to founder events and lack of incoming gene flow. Any effects due to climate are controlled for in the sampling design.

Materials and methods

THE SPECIES

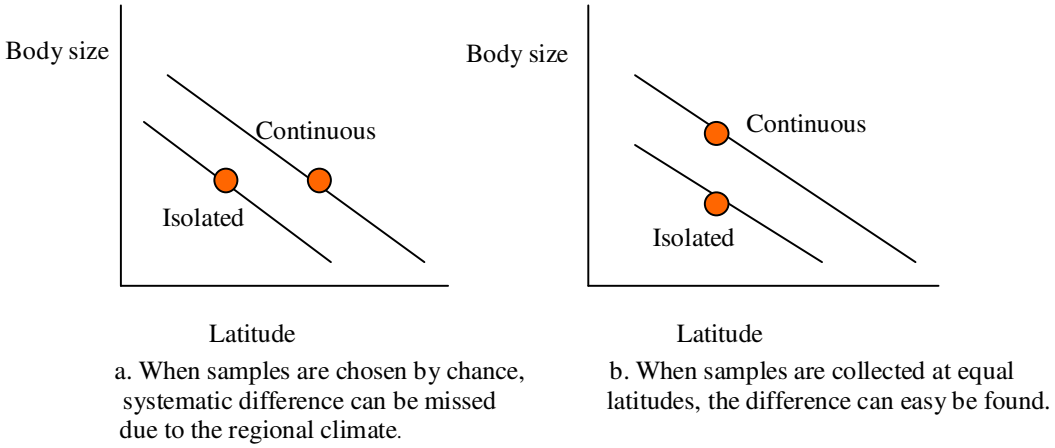
Roesel's bush cricket is a small, generally short-winged species, 12–18 mm in length (Bellmann, 1985). About 1 % of the population is long-winged, i.e. macropterous (Vickery, 1965). It prefers moist and ungrazed tall grass habitat where it feeds on vegetation, seeds and small insects (Marshall, Haes, 1988). Between July and October, when the weather is sunny and warm, adult males almost continuously stridulate to attract females. The eggs are laid during summer and autumn and hatch in May, 1-2 years later (Ingrisch, 1986). The nymphal development consists of 5-6 instars before they become adults in July and August (Marshall, Haes, 1988).

Metrioptera roeselii is common and widespread in the continental part of Europe (de Jong, Kindvall, 1991; Harz, 1957; Ingrisch, 1986), while in Sweden, *M. roeselii* was unnoticed until about 100 years ago. The earliest report of *M. roeselii* is from 1882, although the species was then unnoticed until 1957 when it was rediscovered in the vicinity of Västerås, where it is believed that they were introduced with a cargo ship (de Jong, Kindvall, 1991). It has its main occurrence around Lake Mälaren although it has expanded and can now be found hundreds of kilometers from Västerås (Pettersson, 1996). Nowadays, it occurs also in a small and isolated site in southern Sweden (Smygehuk) (Ahlén, 1995) and at restricted sites in northeast Sweden (Skellefteå, Umeå, Luleå and Haparanda) (www.artportalen.se). On the Baltic Sea island Åland, *M. roeselii* is common (de Jong, Kindvall, 1991) while there are no data available on its abundance on Saaremaa. In Denmark, the species is rare, but has been known for a long time in Lolland (southeast Denmark); the first record was from 1887 (Bavnhoj, 1996) while it was later also found in isolated populations in Falster (southeast Denmark) and Jutland (west Denmark) (Delphin, 1983). The distribution of this species is increasing and in Sweden it appears to out-compete the native Bog bush cricket *Metrioptera brachyptera*, which is being forced into less preferred habitat (Berggren, Low, 2004).

SAMPLING

Sampling sites were chosen as latitudinal pairs (figure 1, table 1). At each latitude I had one sample representing an isolated population and one sample representing one population from the continuous part of the species distribution (figure 2). Specific sites in Sweden were identified from www.artportalen.se which is an open database for the public to report observations of different species and verified regarding the accuracy of known localities by Oskar Kindvall the Ortoptera expert at Swedish Species Centre (Swedish; Artdatabanken). Sites in Denmark, Åland and Saaremaa were identified from

published information (Karjalainen, pers. comm. and Bavnhoj, 1996), and sites within the continuous area were chosen to match the isolated ones.



a. When samples are chosen by chance, systematic difference can be missed due to the regional climate.

b. When samples are collected at equal latitudes, the difference can easy be found.

Figure 1. The importance of collecting samples at equal latitude.

Adult individuals were collected in August and September 2008 with the aim to collect equal numbers of males and females and at least 12 individuals of each sex per site. Males were found through listening and locating their song, while females that do not stridulate were found through visual searching. The sampled individuals were put singly in ID marked 2 ml plastic cryo tubes with screw cap filled with conserving liquid 99.7% ethanol, which killed the bush crickets within seconds.

MORPHOLOGY MEASUREMENTS

The selected traits were chosen so that they i) reflected the size of the individuals, ii) they should be easy to measure and iii) they should have clear start and end points. Finally, ten traits were chosen and included hind tibia length, hind femur length, hind femur width, wing length, head width, thorax (pronotum) length, thorax (pronotum) width, ovipositor length for females / cercus length for males, body length and body weight (figure 3). The left body part was measured unless this was missing, then the right one was measured instead. Only short winged individuals were included in the analyses since long winged individuals may differ in their overall size from short winged ones. All linear traits were measured with a digital slide caliper, having an error of measurement of ± 0.03 mm. Body weight was measured on an electronic balance with an error of measurement of ± 0.1 mg. Individuals who had a hind leg missing were not weighted. Since males and females are known to differ in overall size, these were measured and analyzed separately. All males and all females were measured by the same person and repeated measures were done initially to a certain agreement among measures.

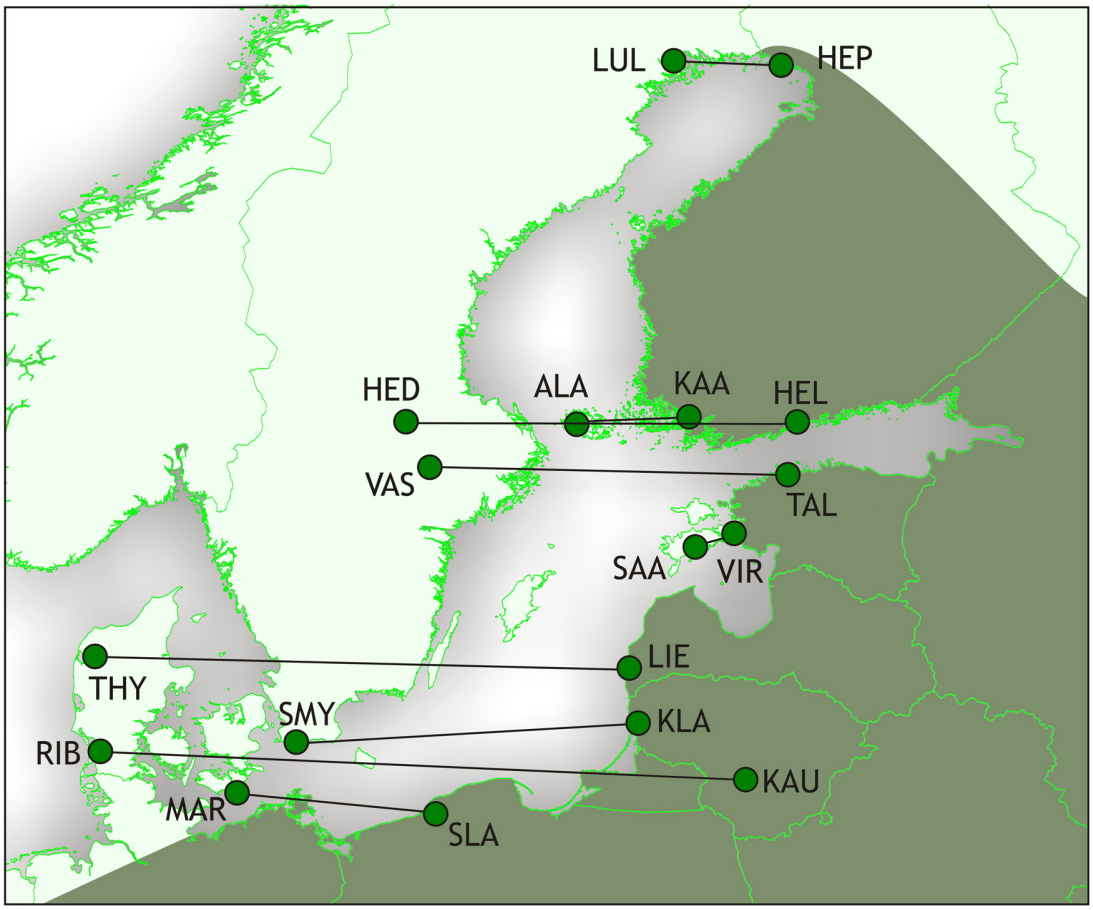


Figure 2. Study area with "latitudinal pairs" where *M. roeselii* was collected. The dark field represents the continuous area of species distribution. The light field represents the isolated area of species distribution and areas where *M. roeselii* is absent.

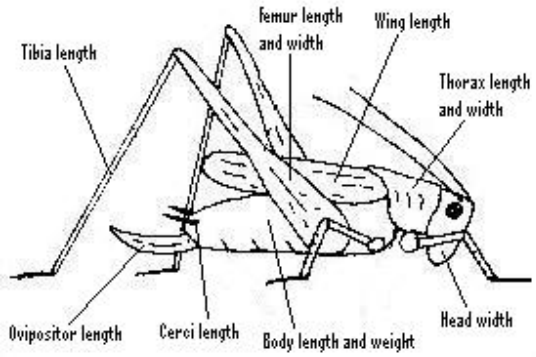


Figure 3. The measured ten traits used in the analyses. The traits are tibia length, femur length, femur width, wing length, thorax length, thorax width, head width, body length, weight and cerci length for males/ ovipositor length for females.

STATISTICAL ANALYSIS

To be included in the statistical analysis, the latitudinal pairs must have at least 4 individuals in each population. This resulted in 4 latitude pairs for females (Marielyst and Slawno, Hedemora and Helsingfors, Åland and Kaarina, Luleå and Hepola) (table 2b) and 8 latitude pairs for males (all pairs but Luleå and Hepola) (table 2a). Sample sizes ranged between 10–23 for males (table 2a) and 4–15 for females (table 2b).

Table 1. Characteristics of each sampled site.

Site	Country	State	Latitude °N	Longitud °E	Distance to coast (km)	Collection date (day/month)
Luleå	Sweden	Isolated	65.73	22.17	4	25/8
Åland	Finland	Isolated	60.26	19.93	11	31/8
Hedemora	Sweden	Isolated	60.26	15.95	88	12/9
Västerås	Sweden	Isolated	59.59	16.48	95	10/9
Saaremaa	Estonia	Isolated	58.37	22.68	10	15/8
Thyholm	Denmark	Isolated	56.65	8.56	20	28/8
Smygehuk	Sweden	Isolated	55.34	13.36	0	30/8
Ribe	Denmark	Isolated	55.29	8.67	1	27/8
Marielyst	Denmark	Isolated	54.65	11.96	0	29/8
Hepola	Finland	Continuous	65.68	24.65	0	3/8
Kaarina	Finland	Continuous	60.43	22.39	3	9/8
Helsingfors	Finland	Continuous	60.23	24.87	3	11/8
Tallinn	Estonia	Continuous	59.52	24.82	1	14/8
Virtsu	Estonia	Continuous	58.57	23.59	1	14/8
Liepāja	Latvia	Continuous	56.54	21.01	1	18/8
Klaipéda	Lithuania	Continuous	55.69	21.14	2	19/8
Kaunas	Lithuana	Continuous	54.85	23.83	162	19/8
Sławno	Poland	Continuous	54.40	16.56	13	21/8

All samples were tested for normal distribution and plotted against latitude to evaluate trends in isolated versus continuous populations. To analyze to what extent individuals in the isolated populations are smaller than individuals in continuous ones, means of all traits of isolated versus continuous populations were tested in a one tailed paired T-test (isolated < continuous). In order to verify that there are differences in means between isolated populations and continuous populations, means of all traits of pooled isolated populations were also tested against means of all traits of pooled continuous populations in a 2-sample T-test.

Table 2. Latitudinal pairs of samples and number of collected individuals (N).
(a) Males and (b) females.

(a)

Isolated	N	Continuous	N
Åland	12	Kaarina	13
Hedemora	10	Helsingfors	15
Västerås	12	Tallinn	23
Saaremaa	23	Virtsu	17
Thyholm	21	Liepãja	21
Smygehuk	14	Klaipéda	23
Ribe	14	Kaunas	22
Marielyst	17	Sławno	15

(b)

Isolated	N	Continuous	N
Luleå	15	Hepola	4
Åland	12	Kaarina	11
Hedemora	6	Helsingfors	9
Marielyst	7	Sławno	9

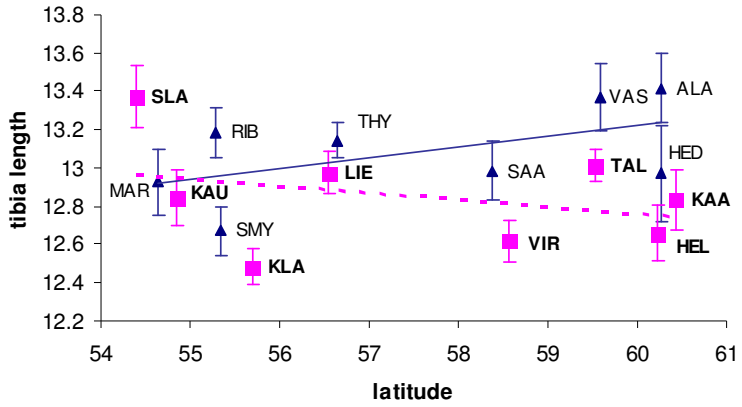
Since it was an apparent difference in geographic trends between isolated and continuous populations I separated GLM analyses for the isolated and continuous datasets.
To consider possible influence of regional climate on variation of body morphology, *distance to coast* and *latitude* were used as factors in the analysis. Due to the small female dataset, only male data was analyzed in the general linear model (GLM) analysis. *Collection date* and *latitude* was set as covariates and *distance to coast* as a fixed factor. *Distance to coast* was measured in GIS and the values classified in 2 levels; 1 = sites which was by or close the coast (0–20 km) and 2 = sites more than 20 km from the coast, i.e. more continental climate. All analyses were performed in the software MiniTab (MiniTab® version 15.1.1.0.).

Results

When analyzing the hypothesis that individuals from isolated populations are smaller than those from continuous ones this was not significantly supported (paired T-test P-values ranging between 0. 48 and 0. 99). However, they appear to differ in latitudinal responses (figures 4 and 5). There are no lines in the plots of females because traits of females did not shows clear latitudinal patterns.
2-sample T-test for males showed that all traits but femur width ($P = 0.860$) and wing ($P = 0.495$) were larger in isolated populations than in continuous ones (P- values ranging between < 0.001 - 0.008) and for females that all traits but tibia length ($P = 0.08$), femur width ($P = 0.139$) and ovipositor length ($P = 0.066$) were larger in isolated populations than in continuous ones (P- values ranging between < 0.001 – 0.05).

When analyzing the isolated and continuous samples separately I found that *latitude* and *distance to coast* explained a large part of the variation in almost all traits for the isolated populations while for continuous ones none of the variables had significant effect (despite for *distance to coast* on wing size in continuous populations) (table 3). *Collection date* did not reach significance neither for isolated nor continuous populations.

(a)



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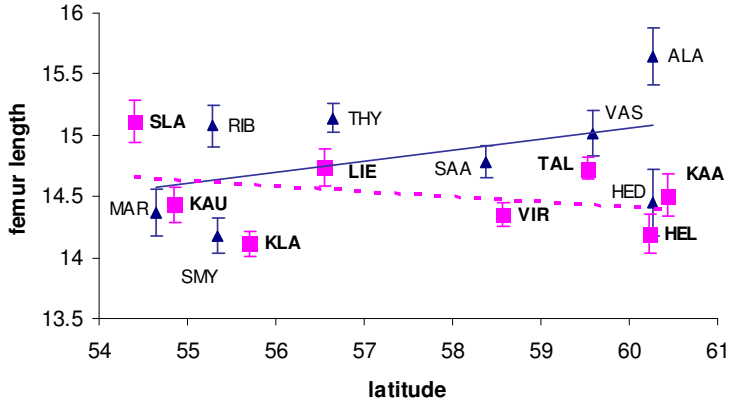

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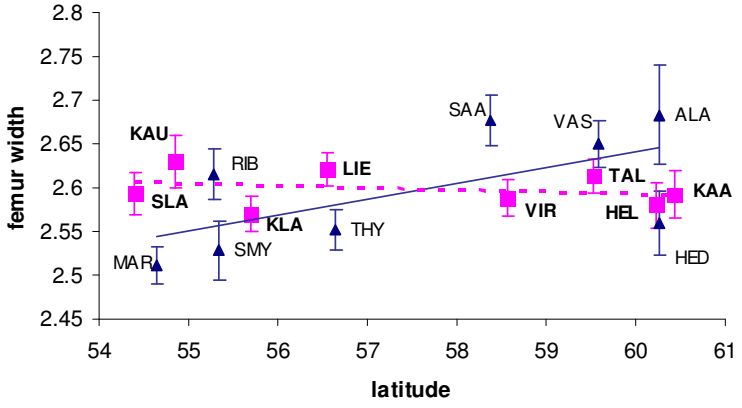
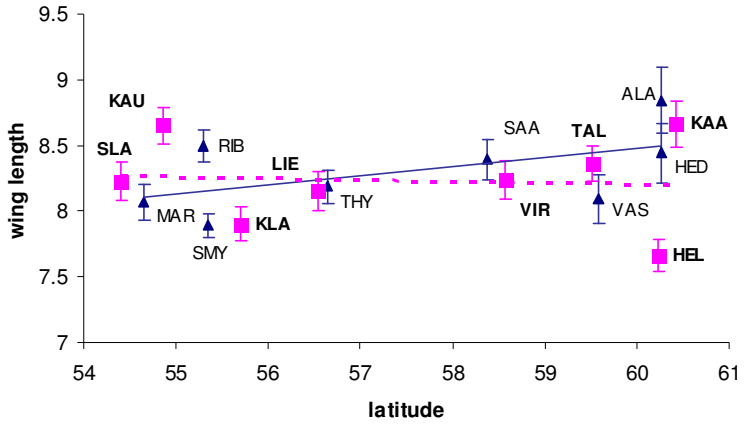


Figure 4. Plots of males. The lines show correlation between a certain trait and latitude within and outside the continuous area. Full line and triangles (▲—) represent isolated samples (outside the continuous area). Crosshatched line and squares (■ --) represent continuous samples. The error bars represent standard error (SE). The presented traits are (a) tibia length, (b) femur length and (c) femur width.

(d)



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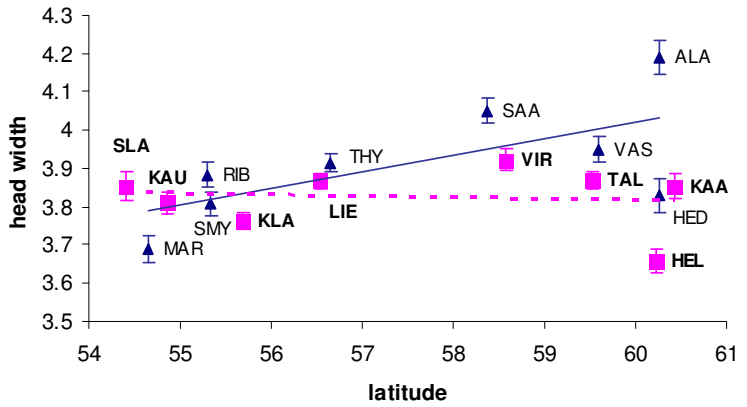

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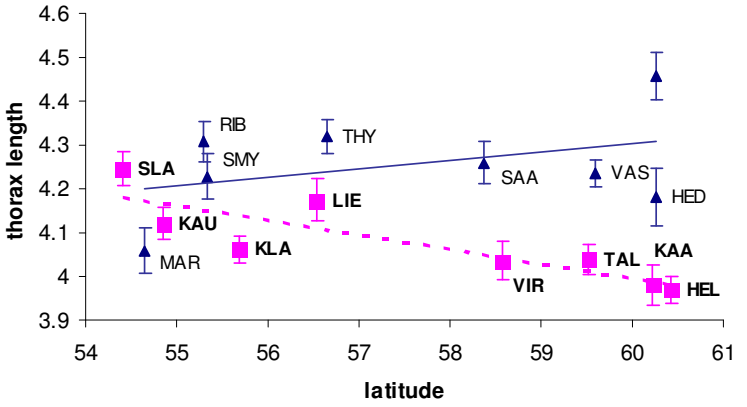
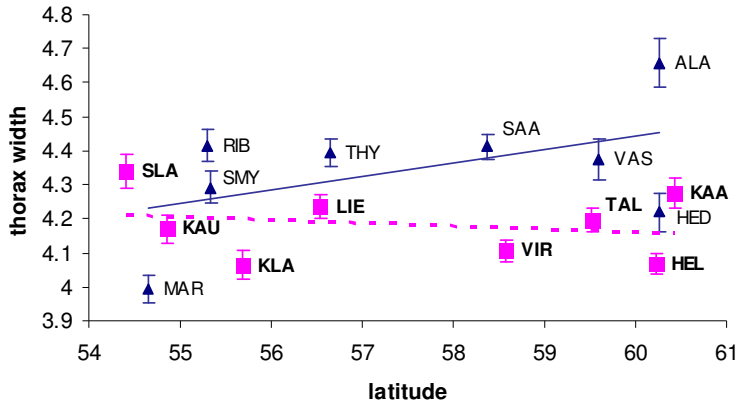


Figure 4. Plots of males. The presented traits are (d) wing length, (e) head width and (f) thorax length.

(g)



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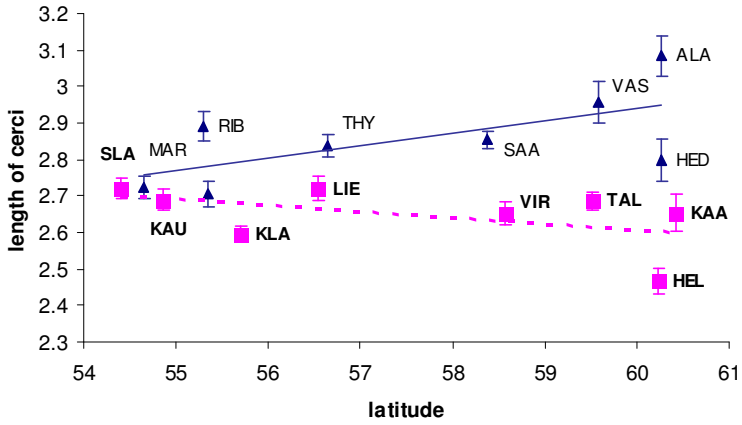


(i)

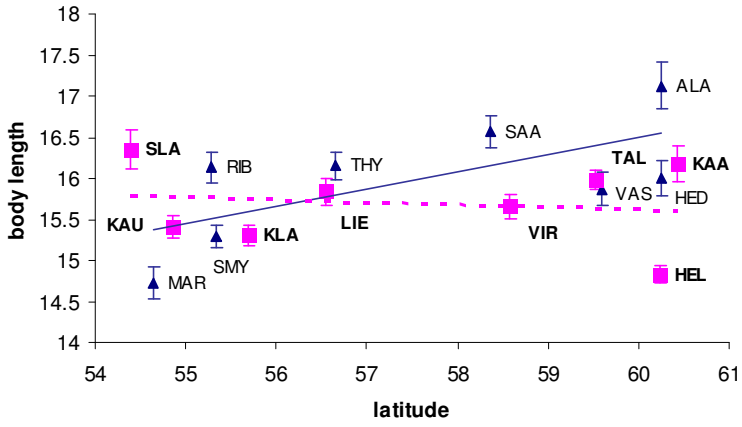


Figure 4. Plots of males. The presented traits are (g) thorax width, (h) cerci length and (i) body length.

(j)

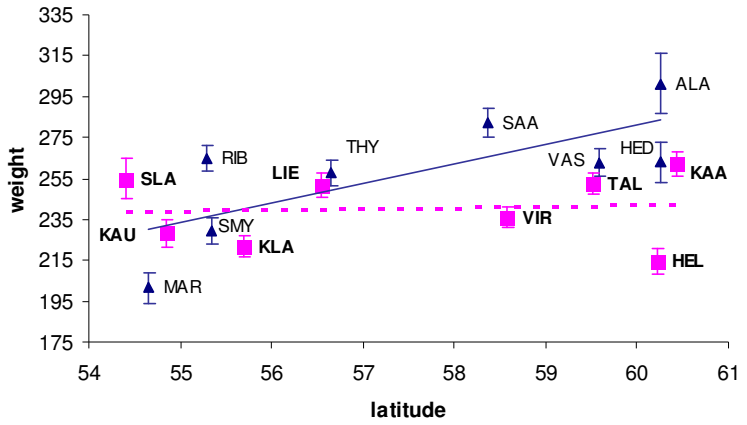


Figure 4. Plots of males. The presented trait is (j) weight.

(a)

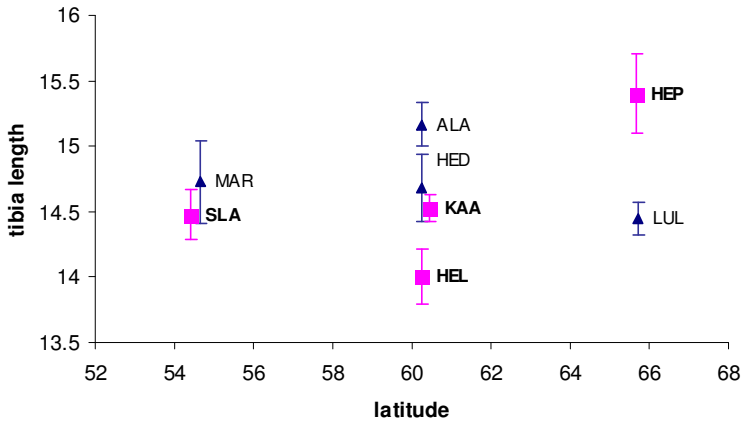
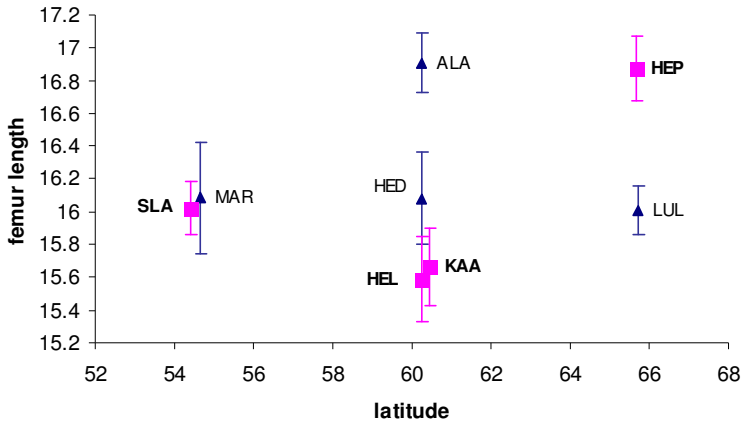


Figure 5. Plots of females. The points show correlation between a certain trait and latitude within and outside the continuous area. Triangles (▲) represent isolated samples (outside the continuous area). Squares (■) represent continuous samples. The error bars represent standard error (SE). The presented trait is (a) tibia length.

(b)



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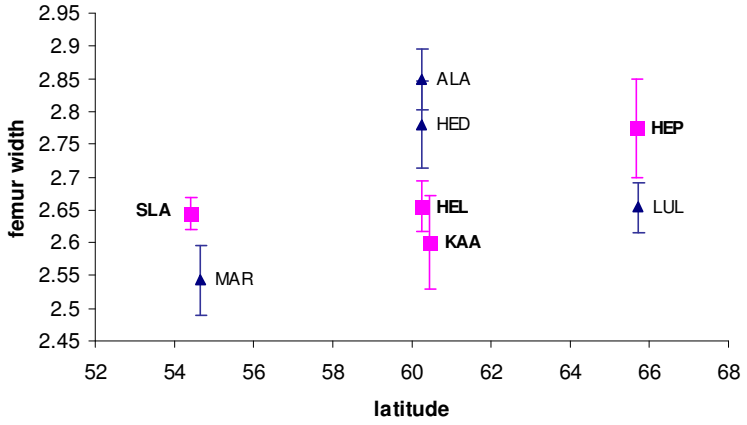


(d)

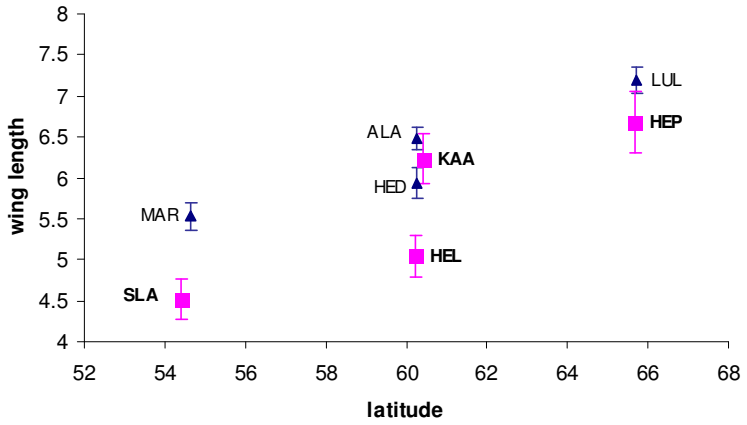
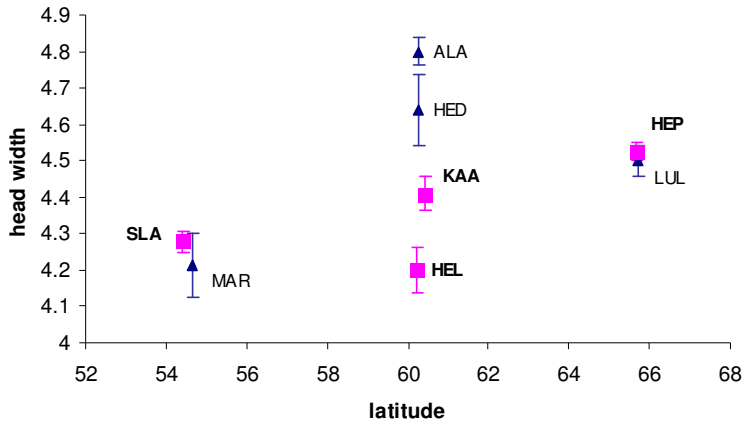


Figure 5. Plots of females. The presented traits are (b) femur length, (c) femur width and (d) wing length.

(e)



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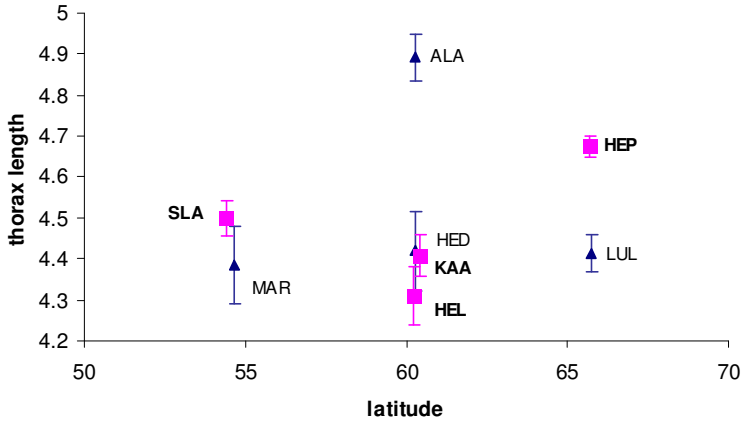


(g)

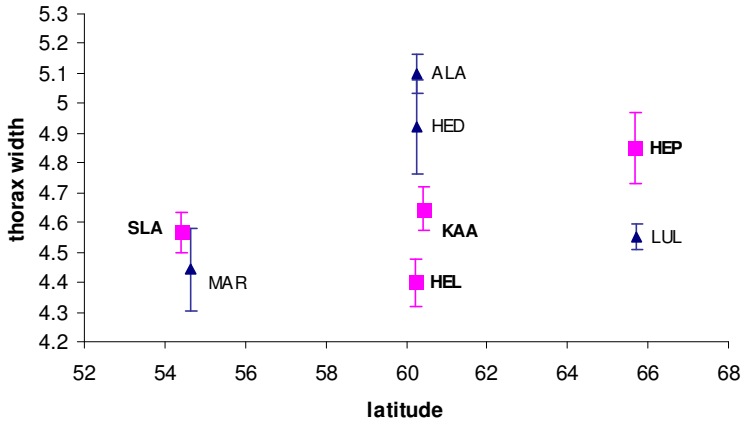
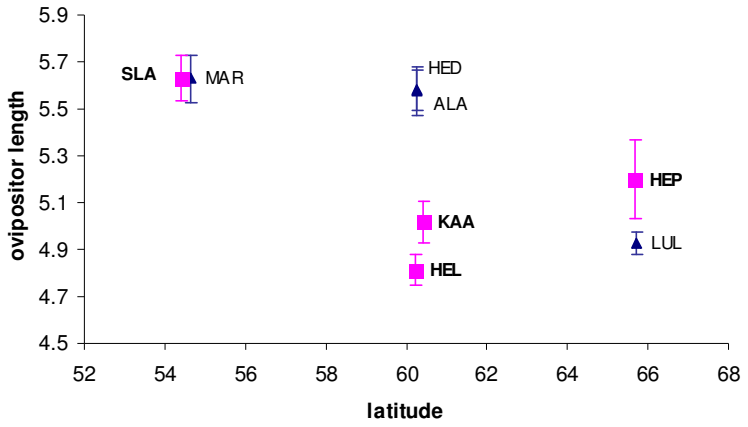
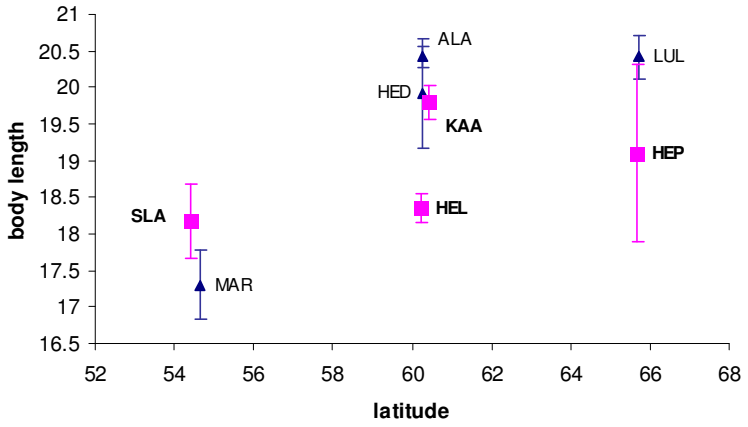


Figure 5. Plots of females. The presented traits are (e) head width, (f) thorax length and (g) thorax width.

(h)



(i)



(j)

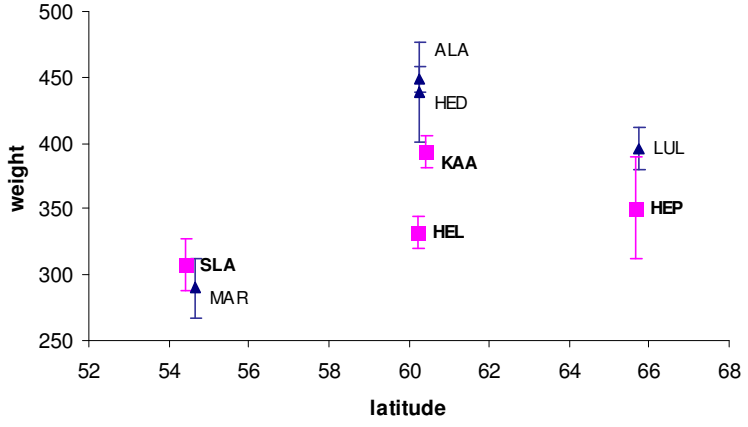


Figure 5. Plots of females. The presented traits are (h) ovipositor length, (i) body length and (j) weight

Table 3. Results of the General linear model analysis of male data including the variables *latitude*, *distance to* coast and *collection date*. Figures in bold indicate significant p-values < 0.05. (a) Isolated and (b) continuous.

(a)

Variable	d.f.	Tibia length	Femur length	Femur width	Wing length	Head width	Thorax length	Thorax width	Cerci length	Body length	weight
Latitude	1	F= 4.24 P= **0.042**	F= 19.83 P< **0.001**	F= 12.15 P= **0.001**	F= 11.71 P= **0.001**	F= 90.21 P< **0.001**	F= 19.46 P< **0.001**	F= 47.85 P< **0.001**	F= 30.62 P< **0.001**	F= 54.95 P< **0.001**	F= 59.78 P< **0.001**
Coll. Date	1	F=1.03 P= 0.311	F= 3.26 P= 0.074	F= 3.80 P= 0.054	F= 0.42 P= 0.518	F= 0.42 P= 0.520	F= 3.16 P= 0.087	F= 1.35 P= 0.247	F= 2.65 P= 0.106	F= 0.25 P= 0.615	F= 1.05 P= 0.309
Distance to coast	1	F=0.92 P= 0.339	F= 9.98 P= **0.002**	F= 0.02 P= 0.900	F= 3.62 P= 0.60	F= 13.86 P< **0.001**	F= 11.99 P= **0.001**	F= 15.53 P< **0.001**	F= 6.82 P= **0.010**	F= 7.72 P= **0.006**	F= 3.31 P= 0.072
R- Sq. (adj.)		1.87 %	12.49 %	14.9 %	7.08 %	46.94 %	12.95 %	28.40 %	19.55 %	34.52 %	40.94 %

(b)

Variable	d.f.	Tibia length	Femur length	Femur width	Wing length	Head width	Thorax length	Thorax width	Cerci length	Body length	weight
Latitude	1	F= 0.61 P= 0.437	F= 0.84 P= 0.362	F= 1.10 P= 0.297	F= 0.05 P= 0.829	F= 0.92 P= 0.339	F= 0.08 P= 0.771	F= 0.97 P= 0.326	F= 0.74 P= 0.391	F= 0.10 P= 0.751	F= 0.03 P= 0.854
Coll. Date	1	F= 1.21 P= 0.274	F= 1.75 P= 0.187	F= 1.01 P= 0.316	F= 0.26 P= 0.613	F= 1.23 P= 0.269	F= 0.82 P= 0.336	F= 0.53 P= 0.467	F= 2.11 P= 0.149	F= 0.00 P= 0.976	F= 0.02 P= 0.894
Distance to coast	1	F= 0.01 P= 0.905	F= 0.18 P= 0.671	F= 3.13 P= 0.079	F= 6.81 P= **0.010**	F= 0.01 P= 0.931	F= 0.35 P= 0.553	F= 0.85 P= 0.358	F= 0.69 P= 0.407	F= 3.07 P= 0.082	F= 1.20 P= 0.275
R- Sq. (adj.)		0.00 %	1.01 %	0.23 %	5.47 %	0.00 %	13.44 %	0.00 %	3.95 %	0.77 %	0.00 %

The total amount of variation that could be explained by the three included variables differed largely among traits and ranged between 1.87 – 46.94 % for isolated area and 0.00 – 13.44 % for continuous area (table 3).

Discussion

The data only allowed thorough analyses of the males and I will therefore limit the discussion accordingly and only briefly discuss the patterns in females.

The results did not follow my expectation that inbreeding in the isolated populations resulted in individuals being smaller than in longer established and non isolated populations. On the contrary, individuals in most of the isolated populations were of equal size or larger than the corresponding continuous ones. Only one population followed my expectation; the sample from Marielyst had smaller individuals than the non isolated one in Slawno. Instead I found two different latitudinal patterns: increasing body size at higher latitudes for isolated samples and no correlation between latitude and size for continuous ones.

There are a number of possible reasons for the larger individuals in isolated populations: they may not experience reduced genetic variation, there may be too few generations as small populations, or inbreeding may not be expressed as reduction in body size.
If size indicates the genetic status of the populations, with larger individuals being more variable, *M. roeselii* manages the isolated situation well. A good colonist is often a generalist and a good competitor (MacArthur, Wilson, 1967) and *Metrioptera roeselii* seems not to be a discriminating species. It can live everywhere where the habitat is humid, i.e. meadows and road ditches (de Jong, Kindvall, 1991) and in Sweden it out-competes the native bog bush cricket *Metrioptera brachyptera* (Berggren & Low 2004). Further, eggs are placed inside leaves of grass, but the species is not bound to any certain grass species (de Jong, Kindvall, 1991) and it has a broad diet (Marshall, Haes, 1988). I suggest that, in a previously unoccupied area where the environment is favourable with good food resource, it may have offered an opportunity for higher growth rate and mean adult body size (Field, Yuval, 1999) as found in isolated populations.

I cannot either exclude that some populations in Scandinavia are young and not yet affected by inbreeding depression. For instance, occurrence of *M. roeselii* in Jutland (where Ribe and Thyholm are located) in Denmark was reported as late as in the 1980's (Delphin 1983) and the population in Smygehuk was found in 1994 (Ahlén 1995). On the other hand, the first observations of *M. roselii* in Åland are from mid 20th century (S. Karjalainen, pers. commun.) and the population appear not to be young. Despite this the individuals were large. If the individuals on Åland had been affected by inbreeding depression, I would expect them to be small. The Marielyst individuals were the only one that followed my expectation and there *M. roeselii* has been known a long time (Delphin 1983).

It is also possible that inbreeding depression is expressed in other traits rather than size. Among insects, traits usually related to fitness are number of offspring, clutch size, egg

development or larval survival (Fox *et al.*, 2007; Henter, 2003; Luna, Hawkins, 2004; Reale, Roff, 2003; Roff, 2002; Saccheri *et al.*, 2005). In contrast to the mentioned traits, I found few papers where reduced body size was correlated to reduced genetic variation (see however Bryant 1986, Saccheri 2001, Kölliker – Ott et al. 2003 and Tran, Cedland 1995). Consequently, it would be more likely to find effects of inbreeding depression when looking at traits more closely associated with fitness.

In addition to the fact that isolated individuals were in general larger, *latitude* and *distance to coast* explained a large part of the variation for isolated populations, but not for the continuous ones (Table 3). I argue that gene flow among continuous populations and the lack of it among isolated ones creates the difference in latitudinal pattern. Gene flow decreases the genetic differentiation betweens populations so that they in reality evolve together (Slatkin, 1994). With significant exchange of individuals among connected populations gene flow from more central ones can inhibit peripheral populations to evolve to local ecological optima, while rapid evolution can occur when a population is suddenly isolated from gene flow (Garcia-Ramos *et al.*, 2002).

One of the best known geographical patterns for animals is the "Bergmann's rule" which means individuals of the same species tend to be larger at higher latitudes. This is generally assumed to be related to thermoregulation, where bigger animals can thermoregulate better in cold areas (Ashton, 2000). Consequently, this is found especially among endothermic mammals and birds (Ashton, 2000). A possible explanation for increasing body size with latitude in insects could rather be that species with short life span are not affected by the length of favourable season but instead of the availability of food resources (Chown, Gaston, 1999) or that cell size in ectotherms grows larger in cold temperature (van Voorhies, 1996). Although *M. roeselii* follows this pattern, among crickets the trend is often the opposite; the size decreases at higher latitude and the pattern is therefore called "converse Bergmann's rule" (Mousseau, 1997; Mousseau, 2000). For example, the striped ground cricket, *Allonemobius faciatus* (Mousseau, 2000) and several Japanese cricket species (Masaki, 1978) follow this pattern. The variation in body size of these crickets reflects variation in the length of the growing season. In the north, this species is producing one generation per year (univoltine) and in the south it produces two generations per year (bivoltine). Body size shows a "sawtooth" pattern, where body size increases from north to south, followed by a rapid decrease in the region of transition from univoltine to bivoltine life cycles. South of the region, the body size increases again due to the increased growing time.

For females, the patterns in the southern latitudinal pairs are like the ones for males. That is, the traits in Åland and Hedemora are of equal size or larger than in Kaarina and Helsingfors and the traits in Marielyst are of equal size or smaller than in Slawno (but not wing length, figure 5 d). For males, the traits in the isolated area are increasing at higher latitudes while the males in continuous population are of more equal size. For females, however, the pattern in the isolated area is more as a "curve"; small in south, larger in middle and in north, they again decrease in size. In the plots of the females, I have samples from Luleå and Hepola which are located at much higher latitude, almost at 66°, while there are no such samples of the males. Thus, males and females are not really

comparable. Concerning the continuous area, females in Hepola are larger than in the southern sites. Only 4 females were caught in Hepola and it is not possible to conclude if the difference is due to chance or the colder climate.

Further, there is another difference between males and females; in the isolated area, the ovipositor length decrease at higher latitude as opposed to the other traits. That is, larger individuals have shorter ovipositor at higher latitude. One speculation is that the ovipositor length depends on the vegetation structure since *M. roeselii* lays eggs into leafs of grasses. That ovipositor size is related to environmental cues are known also from other species. For example in crickets where females lay eggs into the ground they have smaller body masses but longer ovipositors. The ovipositor length is then assumed to be correlated with the depth at which eggs are deposited into the ground, i.e. the colder temperature the deeper the eggs are deposited in the ground (Mousseau, 2000). In the leaf beetle *Plateumaris constricticolli,* females with short ovipositor can lay eggs in thin grass stems while females with long ovipositor have to lay eggs into thick grass stems. The ovipositor length thus differs between different areas depending on the vegetation (Sota *et al.*, 2007).

Genetic information will allow conclusions whether *M. roeselii* in isolated populations has reduced genetic variation and will also allow us to identify where the populations originate from as well as provide information about their ages. More detailed data about the species distribution around the range margin in Germany, Denmark and northern Sweden will also verify the level of isolation for the populations found there. In the future, it would be interesting to study habitat characteristics like soil characteristics, plant structure and diversity, precipitation, moisture, other species and landscape composition (structure and degree of isolation) in relation to the body measures. Knowledge about the habitat and surrounding landscape in relation to body characteristics can enhance our understanding how the environment affects newly established populations. Finally, it would be interesting to study also females in detail since they differ from males in sex organ and overall size and have different behaviour in the wild; the females lay eggs while the males stridulate. Thereby, females can prioritize and develop different adaptations than males.

Conclusions

No trait, neither for males nor females in isolated populations was on average smaller than in continuous populations. On the contrary, they tended to be larger. The possible explanation why *M. roeselii* seems to manage the isolated situation well is that it is a sustainable species being a generalist and good competitor. In addition to isolated individuals being larger than in the continuous ones, the latitudinal patterns in the two areas differ; there was a gradual increase in size at higher latitude in isolated populations while in continuous populations they were of equal size at all latitudes. I believe that this is due to the gene flow among continuous populations while there is no gene flow among isolated populations allowing them to reach regionally ecological optima. I cannot from

current data conclude the mechanisms for this pattern and further studies are needed to draw through conclusions.

The results from this study can be used in future studies about how alien species establish and generate knowledge about processes of colonising species.

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